IDENTIFICATION OF *PURSHIA SUBINTEGRA* (ROSACEAE)

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ABSTRACT.—Populations of *Purshia* in central Arizona are intermediate in some characters between *Purshia subintegra*, an endangered species, and *Purshia stansburiana*, the common cliffrose. These intermediates may represent forms derived from a history of hybridization and introgression between the putative parent species. Morphological data were obtained from 216 pressed specimens of *P. subintegra*, *P. stansburiana*, and introgressed forms. Over 50 separate discriminant function analyses (DFA) and principal components analyses (PCA) were run on numerous combinations of raw and log-transformed data. The best variable suite, providing the clearest discrimination between groups, used log-transformed data on 15 morphological characters, but DFA post-hoc identifications were 90–100% correct with only 7 characters using raw data. DFA distinguished four separate nodes of variation. Two groups consisting of 122 *P. subintegra* and 29 *P. stansburiana* were easily discriminated in DFA and were distinguished in PCA as well. Introgressed forms were consistently identified in two much less well-defined groups of 46 and 19 specimens. Introgressed forms are not intermediate between the two supposed parents in some characters, appearing most similar to *P. stansburiana* in most measured characteristics. Principal distinguishing characteristics of the four groups are as follows: *P. subintegra*—usually eglandular, has 0–2 leaf lobes and short hypanthia-pedicels; *P. stansburiana*—always abundantly glandular, has 4 leaf lobes and short hypanthia-pedicels; the introgressed form "Tonto" is usually eglandular, has 4 leaf lobes and long hypanthia-pedicels; the introgressed form "Verde" is usually glandular, has 4 leaf lobes and slightly shorter hypanthia-pedicels.

Key words: *Purshia subintegra, Purshia stansburiana, Arizona cliffrose, cliffrose, endangered species, morphometrics, introgression, taxonomy,*

Purshia subintegra (Kearney) Henrickson (Arizona cliffrose) is protected under federal law as an endangered species (USFWS 1984). For a federally endangered species like *P. subintegra* it is important, indeed vital, to know the taxonomic identity of every individual plant in a given population because the protective measures of the Endangered Species Act are available to species (including forms that exhibit characteristics of introgression with other species), but not to their early generation hybrids.

Purshia subintegra is found in four widely scattered locations from northwestern to southeastern Arizona (Table 1, Fig. 1). The first collection was made by Darrow and Benson in 1938 (Kearney 1943, Schaack 1987a) near Burro Creek in Mohave County, Arizona. A second population was documented in a collection by Pinkava, Keil, and Lehto in 1968 (Pinkava et al. 1970) almost 300 km from Burro Creek, near Bylas in Graham County, Arizona. Anderson (1986) found a third population on bluffs overlooking the upper Verde River near the town of Cottonwood (referred to as the Verde Valley area) and reported on

Barbara G. Phillips' 1984 discovery of the fourth locality for *P. subintegra* near Horseshoe Dam along the lower Verde River.

At the four locations cited above, *Purshia subintegra* is restricted to outcrops of Tertiary deposits of limy lacustrine rock formations (Anderson 1986). Soils derived from these ancient lake basin rocks are characterized by low nitrogen and phosphorus levels, which limit, or preclude, typically Sonoran Desert species that are common on nearby sites with soils derived from igneous and metamorphic rocks (Anderson 1986). *Purshia subintegra* is a species of the northern and eastern perimeter of the Sonoran Desert; all four sites supporting the species are at or below 1000 m elevation.

Purshia stansburiana, the common cliffrose of the Southwest, is not a Sonoran Desert species and consequently is not sympatric with *P. subintegra* at three of the four *P. subintegra* sites known. In the Verde River Valley of eastern Yavapai County, Arizona, the highest-elevation *P. subintegra* site, the two species occur in close enough proximity that gene exchange may occur, at least occasionally. Scattered populations and individuals of

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TABLE 1. Locations of *Purshia* spp. collections sampled in multivariate morphometric analysis; 216 specimens collected for morphological analysis in Arizona.

Region and collection site	N	County	Letter designation	Elev. (m)	Biotic community	Substrate
			Purshia subintegra			
1. Bylas	20	Graham	A	850	Sonoran desertscrub	Tertiary lacustrine
2. Burro Creek	20	Mohave	B	790	Sonoran desertscrub	Tertiary lacustrine
3. Horseshoe Lake	42	Maricopa	C	640	Sonoran desertscrub	Tertiary lacustrine
4. Verde Valley	8	Yavapai	D	1025	Semidesert grassland	Verde Formation
5. Verde Valley	24	Yavapai	E	1050	Semidesert grassland	Verde Formation
6. Verde Valley	8	Yavapai	F	1065	Semidesert grassland	Verde Formation
			"Verde"			
Verde Valley						
7. DK Well Rd.	3	Yavapai	a	1185	Semidesert grassland	Verde Formation
8. Seventeen Tank Rd.	6	Yavapai	b	1020	Semidesert grassland	Verde Formation
9. Mesa Blanca	3	Yavapai	c	1210	Semidesert grassland	Verde Formation
10. DK Well Rd.	1	Yavapai	d	1175	Semidesert grassland	Verde Formation
11. DK Well Rd.	3	Yavapai	e	1155	Semidesert grassland	Verde Formation
12. Seventeen Tank Rd.	3	Yavapai	f	1035	Semidesert grassland	Verde Formation
13. Cottonwood Hwy.	1	Yavapai	g	1030	Semidesert grassland	Verde Formation
14. Cornville	2	Yavapai	h	1110	Semidesert grassland	Verde Formation
15. Black Mtn. Rd.	6	Yavapai	i	1385	Piñon-juniper woodland	Supai Formation
16. Cherry Rd.	3	Yavapai	j	1070	Semidesert grassland	Verde Formation
17. Cherry Rd.	3	Yavapai	k	1230	Interior chaparral	Verde Formation
18. Cherry Rd.	6	Yavapai	l	1270	Interior chaparral	Verde Formation
19. Cherry Rd.	6	Yavapai	m	1341	Interior chaparral	Verde Formation
			"Tonto"			
Verde Valley						
20. Camp Verde	2	Yavapai	n	990	Interior chaparral	Verde Formation
South of Globe						
21. Dripping Springs Rd.	6	Gila	o	990	Semidesert grassland	Limestone?
Tonto Basin						
22. Pinal Creek	3	Gila	p	944	Semidesert grassland	Tertiary lacustrine
23. Punkin Center	6	Gila	q	725	Sonoran desertscrub	Tertiary lacustrine
24. Beeline Hwy.	2	Gila	r	1015	Interior chaparral	Tertiary lacustrine
			Purshia stansburiana			
25. Jerome	16	Yavapai	X	1770	Interior chaparral	Tertiary basalt
26. Skull Valley	3	Yavapai	Y	1270	Semidesert grassland	Weathered volcanics
27. Sonoita	10	Santa Cruz	Z	1435	Plains grassland	Quaternary alluvium

Purshia in central Arizona exhibit what appear to be intermediate characteristics between *P. subintegra* and *P. stansburiana*. Numerous botanists (Schaack and Morefield 1985, Schaack 1987a, 1987b, Anderson 1986, 1993, Henrickson personal communication 1988) have assumed that intermediate forms arose from past hybridization and subsequent introgression with one or both of *P. subintegra* and *P. stansburiana*, and that hybridization and introgression may still be occurring in some locations. Throughout this paper the term "introgressed form," recognizing that the origin of the intermediates is still unclear, is applied to forms that are intermediate in some characters between *P. subintegra* and *P. stansburiana*.

Related Taxa

The systematics of *Purshia* is under investigation by Dr. James Henrickson for the upcoming Chihuahuan Desert Flora and the revised Arizona Flora. Henrickson (1986) published a brief note recombining species previously placed in *Cowania* to *Purshia*, a move generally agreed upon by botanists. Thus, the genus *Purshia* now consists of seven species: *Purshia ericifolia* (Torr. ex Gray) Henrickson, *P. glandulosa* (Curran), *P. mexicana* (D. Don) Henrickson, *P. plicata* (D. Don in Sweet) Henrickson, *P. stansburiana* (Torr. in Stansb.) Henrickson, *P. subintegra* (Kearney) Henrickson, and *P. tridentata* (Pursh) DC. Although the
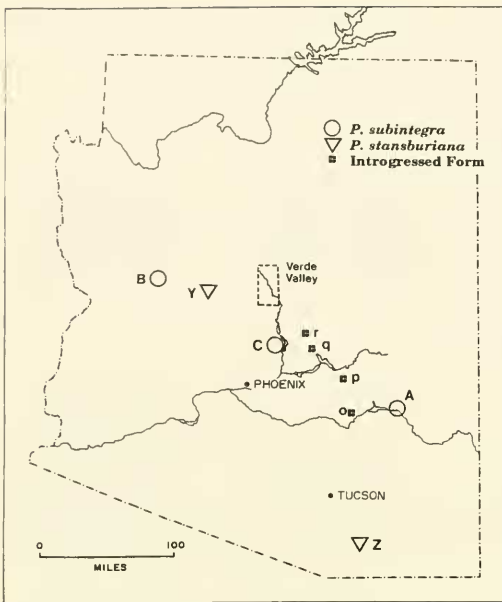
Fig. 1. Distribution of sampling sites, species, and introgressed forms. See Figure 2 for an expanded view of Verde Valley. Letters identify sites illustrated in graphs of multivariate analyses.

relationship of *P. subintegra* to *P. stansburiana* is the subject of this study, that of *P. subintegra* to the morphologically similar *P. ericifolia* is of interest as well. All other *Purshia* taxa have lobed leaves except *P. ericifolia*. Leaves of *P. ericifolia* are about 6 mm long, simple, acute, linear, and eglandular. The species is restricted to limestone outcrops in the Texas Big Bend region. It has been speculated that *P. subintegra* may have evolved from some ancient series of crosses and backcrosses involving *P. ericifolia* and some other *Purshia*, perhaps *P. stansburiana* (McArthur et al. 1983). Phylogenetic investigation of the whole genus in relation to closely related genera such as *Fallugia* would be valuable in interpreting *P. subintegra* and should be the logical next step for future work.

Relation to *Purshia stansburiana*

Schaack (1987a, 1987b) suggested that the basionym *P. subintegra* was based on material of hybrid origin, resulting from past hybridization of *P. stansburiana* and a previously unnamed central Arizona *Purshia*. He consequently published a new species name, *Purshia pinkavae* Schaack, to include a very pure concept of what had been included in *P.*

subintegra, ". . . restricted to late Tertiary calcareous, lacustrine deposits ca. 16–21 km northwest of Bylas, Graham County, Arizona."

Few botanists have adopted Schaack's taxonomy, but most recognize that variation is present and concede that it may have resulted from some form or degree of past hybridization or introgression involving *P. subintegra* and *P. stansburiana*.

McArthur et al. (1983) reported n = 9 and 2n = 18 for *P. subintegra* and *P. stansburiana*, respectively. Phillips et al. (1988) used starch gel electrophoresis to investigate isozymes at 14 loci in three populations of *Purshia stansburiana* and four populations of *P. subintegra*. The material used in this study was collected by the author and preserved in liquid nitrogen from the same plants that provided dried specimens for this study. Phillips et al. (1988) were unable to discern differential patterns of variability useful in identification of taxonomic groups; between-groups similarities ranged from 0.925 to 0.992 (Nei [1978] unbiased genetic identity).

Fitts et al. (1992) studied *Purshia subintegra* in Verde Valley, reporting on many important, but heretofore unknown, aspects of the pollination biology of the species. They found that flowers may be pollinated anytime in the first three days after anthesis, the plants are partially self-compatible, and native and introduced bees are primary pollinators. Reciprocal crossing experiments between *P. subintegra* and what was believed to be *P. stansburiana* were also conducted by Fitts et al. (1992). As is discussed in the concluding section of this report, plants from which the *P. stansburiana* was taken are actually introgressed forms.

The purpose of this study was to analyze morphological character variation in species of *Purshia* in order to identify the range of morphological variation in *P. subintegra* and to develop a means of discriminating between *Purshia subintegra*, an endangered species, and other non-endangered *Purshia* taxa with which *P. subintegra* is most likely to be confused. This study was undertaken solely to address the need of natural resource managers to have a means of determining which individuals and populations of *Purshia* are protected under the Endangered Species Act. The methods used in this study were carefully chosen to obtain this result.

METHODS

A total of 216 *Purshia* plants were sampled at 27 widely scattered sites from southeastern to northwestern Arizona for measurement and analysis of morphometric characters (Fig. 1). Much attention was given to sampling *Purshia* in Verde Valley, the only location where it is believed *P. subintegra* and *P. stansburiana* are in close enough proximity that gene exchange might currently be occurring. It was hoped that if hybridization were occurring between the two taxa, it would be possible to isolate characters useful in discriminating between *P. subintegra*, *P. stansburiana*, and the introgressed forms. In determining where to sample, it was important to have some firsthand notion of where the introgressed forms might be: this turned out to be more difficult than it might seem given the disparate views of several researchers. Table 1 lists three separate collection sites for *P. subintegra* in Verde Valley (labeled **D**, **E**, and **F**), in addition to several locations for introgressed forms and one location for *P. stansburiana* on mountains overlooking the valley (Jerome, labeled **X**). Figure 2 shows Verde Valley and collection sites in the valley. The author made three separate collecting trips to Verde Valley—1987, 1989, and 1992—each time expanding the scope of the sampling effort to try to obtain a more representative sample of character variation.

Morphometric samples from each of the 216 sampled plants consisted of two to four 20–40-cm-long branches dried in a standard herbarium press. Samples were collected in April 1987, 1989, and 1992 from each of 4 *P. subintegra* populations, 3 *P. stansburiana* populations, and 20 sites of introgressed forms. Table 1 shows the locations and sample sizes of each collection site. A rigorous stratified-random sampling method was employed at the *P. subintegra* and *P. stansburiana* sites, and at least 10 specimens were collected at each site. Collections at the introgressed form sites were made much more subjectively and the sample sizes were much smaller, only one to six specimens.

Data on 15 characters judged to be potentially useful in taxonomic differentiation between the 27 groups were obtained from the pressed specimens. Floral characters were heavily relied on, and characters that could be used in field identification of unknown speci-mens were also employed. Table 2 shows the character palette developed for the morpho-metric analysis. The list of characters indicates that a mix of binary, categorical, and continuous data was used. This was taken into account in subsequent statistical analyses. All measure-ments and counts were made under a binocu-lar dissecting microscope with a micrometer disk or electronic calipers. Scoring procedures are described in Table 2.

SYSTAT version 4.0 was used to subject the data to more than 50 separate discriminant function analyses (DFA) and principal compo-nents analyses (PCA) to identify morphologi-cal groups and to determine which characters could be most confidently used to separate the groups. Numerous combinations of characters were used to group like data (binary, categori-cal, and continuous) and to examine the effects of including ratios as characters (hypanthium-pedicel length/width, sepal length/width, petal length/width) in the data set. Initial analyses using PCA were run on several combinations of characters to identify characters responsible for within-group similarity.

A priori assignments of plants to groups required for DFA involved grouping collec-tion sites in several combinations by morpho-logical, geographical, and ecological criteria. Most DFAs were run with the following groupings: (1) **27-group analysis**, all 27 collec-tion sites coded as separate groups; (2) **3-group analysis**, 4 *P. subintegra* sites, 3 *P. stans-buriana* sites, and all introgressed forms in one group; (3) **4-group analysis**, 4 *P. subintegra* sites, 3 *P. stansburiana* sites, and the intro-gressed forms separated into two groups iden-tified as "Tonto" and "Verde."

RESULTS

Purshia subintegra can be differentiated from *P. stansburiana* and introgressed forms by leaf glandularity and leaf lobing. The mean score of leaf glandularity in *P. subintegra* is less than 0.4, and the mean number of lobes/leaf is 2.5 or less. All others are more glandular or have more leaf lobes. A population of what I initially believed to be introgressed forms at site a (Fig. 2) in Verde Valley possesses glan-dularity and lobing characteristics of *P. subin-tegra* and, based on this and the results of the multivariate analyses, should probably be clas-sified as *P. subintegra*.
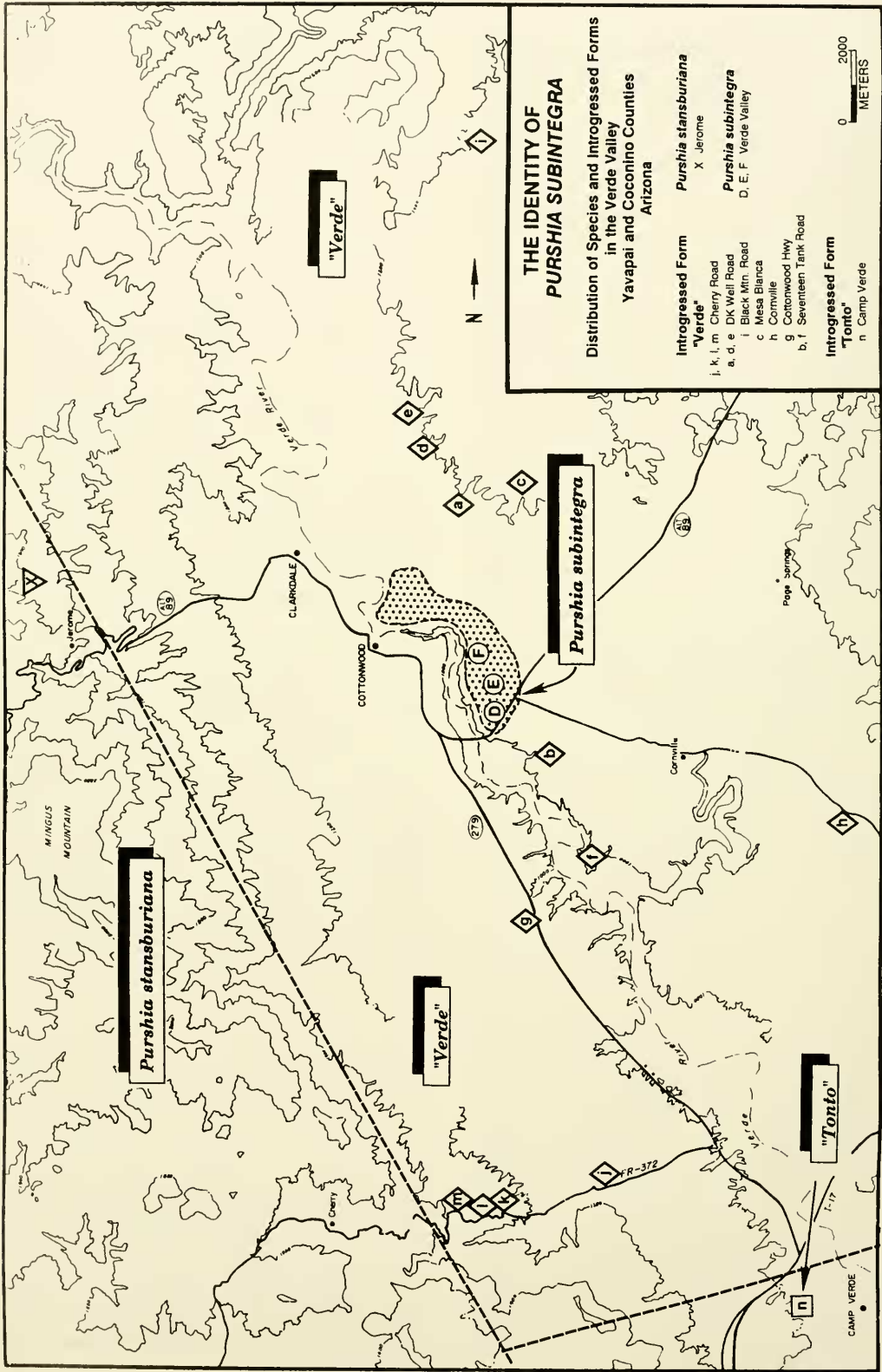
Fig. 2. Distribution of sampling sites, species, and introgressed forms in Verde Valley, Yavapai Co., Arizona.

TABLE 2. Characters measured for analysis of character variation in *Purshia stansburiana*, introgressed forms, and *Purshia subintegra*. Descriptions of the character measurements used in multivariate analyses and acronyms (in parentheses) used as variable labels in Tables 4 and 5. Most hypanthia-pedicel, petal, sepal, pistil, and stamen measurements and counts were from the same five flowers from each plant.

1. **Leaf pubescence.** (LEFPUB) The adaxial surface of *Purshia* leaves is densely tomentose, though the midvein is often bare. The abaxial surface ranges from completely glabrous to completely obscured by long arachnoid hairs. Twenty leaves from each of the 216 plant specimens were scored on an index of leaf pubescence density. Only the dorsal (abaxial) surface was scored. The scale ranged from 1 (completely to nearly completely glabrous) to 5 (densely pubescent).

2. **Leaf glands.** (LEAFGLAN) Ten leaves from each of the 216 plants were examined and scored for presence or absence of impressed-punctate glands.

3. **Hypanthium-pedicel glands.** (HYPGLAN) Five hypanthia (with pedicels) from each plant were examined and scored for presence or absence of stipitate glands.

4. **Leaf lobes.** (LOBES) The number of lobes on each of 20 leaves from each of the 216 plants was counted. The leaf tip was not counted. Lobes varied in distinctness, i.e., from much longer than wide to mere bumps on the edge of the leaf. Even the most minor lobes were scored. Figure 3 illustrates variation in leaf lobing among *P. subintegra*, the "Tonto" and "Verde" introgressed forms, and *P. stansburiana*, and provides an example of lobe scoring.

5-7. **Hypanthium-pedicel dimensions.** (HYPLGTH, HYPWDTH) Length and maximum width of five hypanthia-pedicels from each of the 216 plants were measured under a binocular dissecting microscope using a micrometer disk or electronic calipers. The length/width ratio was also entered as a character variable (HYPRAT).

8-10. **Sepal dimensions.** (SEPLGTH, SEPWDTH) All sepals (usually 5) from five flowers from each of the 216 plants were dissected and measured under a microscope using a micrometer disk or electronic calipers. Maximum (basal) width and length of the sepals were recorded. The length/width ratio was also entered as a character variable (SEPRAT).

11-13. **Petal dimensions.** (PETLGTH, PETWDTH) All petals (usually 5) from five flowers from each of the 216 plants were dissected and measured under a microscope using a micrometer disk or electronic calipers. Maximum width and length of the petals were recorded. The length/width ratio was also entered as a character variable (PETRAT).

14. **Pistil number.** (PSLSFLR) Flowers normally contained 2–4 pistils. Aborted pistils were easily distinguished by their small size (<1.25 mm long) and brown to dark brown color. Viable pistils were pale yellow with silvery-white achene hairs and were nearly always longer than 1.25 mm. The total number of pistils per flower was counted on each of the 216 specimens, as well as the number of viable and aborted pistils.

15. **Number of stamens.** (STMNS) Stamens were counted in five flowers from each of 216 plants.

Table 3 lists mean values and standard errors obtained for each of the 15 characters included in the analysis for each of the four identified groups of *Purshia* spp. Figure 4 illustrates the distribution of variation in sepal and hypanthium-pedicel dimensions. Note that sepal length and width are highly and positively correlated among groups, while hypanthium-pedicel width and length are not. *P. subintegra* plants have shorter, narrower sepals, while *P. stansburiana* have longer, wider sepals; introgressed forms are intermediate. "Tonto" forms have very long, wide hypanthia-pedicels, while "Verde" forms have slightly shorter, but much narrower, hypanthia-pedicels; neither of the two introgressed forms is intermediate in hypanthium-pedicel dimensions between the supposed parent species, *P. subintegra* and *P. stansburiana*.

Principal Components Analysis

Rotated factor scores derived from three PCAs are listed by character in Table 4 and are graphed in Figure 5. The first three factor axes together account for 73–87% of variance in the data. Horizontal relationships on the FACTOR(2)/FACTOR(1) graphs for each analysis (x-axis, Figs. 5A–5C) are primarily based on leaf lobing, while vertical relationships are based on glandularity. The horizontal relationship is again based on glandularity in the FACTOR(3)/FACTOR(2) graphs (y-axis, Figs. 5A–5C), but the vertical relationship (z-axis, Figs. 5A–5C) is mostly influenced by hypanthium-pedicel length.

PCAs illustrate similarities of the three groups of *Purshia* spp. to each other, but graphs must be interpreted carefully. It appears that
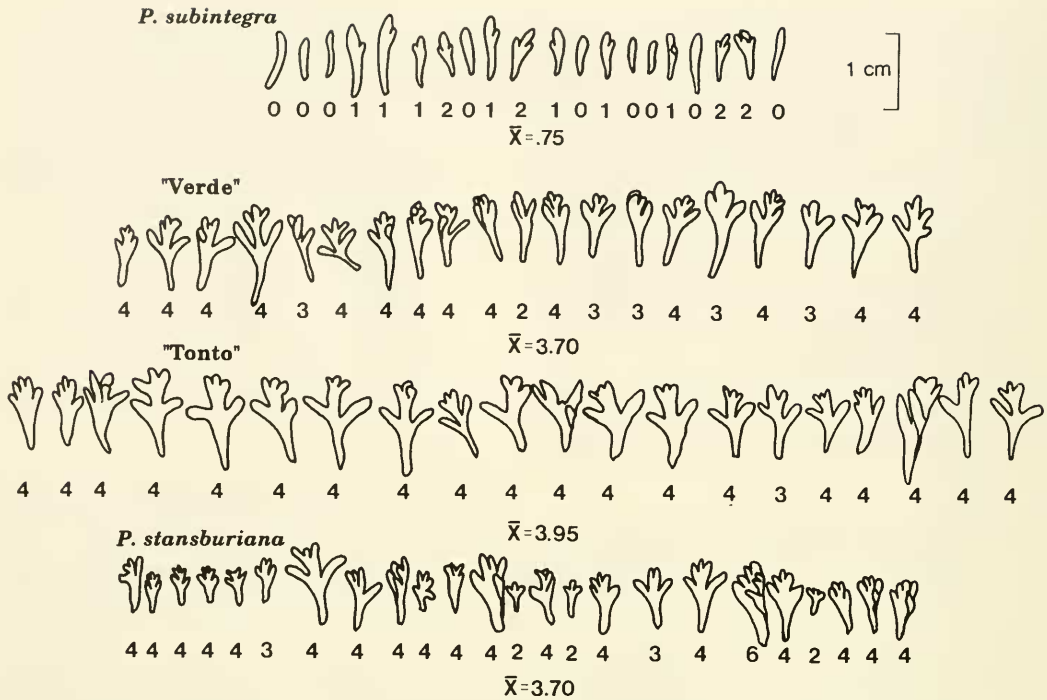
Fig. 3. Variation in leaf lobing and size in *Purshia subintegra*, "Verde" and "Tonto" introgressed forms, and *Purshia stansburiana*. Arrays of 20 leaves scored for pubescence, glandularity, and lobing from typical specimens in each group. Number of leaf lobes scored for each leaf and mean score for each plant are shown.

P. stansburiana groups (X–Z) are lost among "Verde" introgressed forms (b, c, d, e, f, g, h, i, k, l, m), but a careful examination of the distribution of points along FACTOR(3) (z-axis) shows that, primarily on the basis of hypanthium-pedicel length, *P. stansburiana* are more similar to each other. *P. subintegra* and *P. stansburiana* groups (A–F and X–Z, respectively) are usually closest to each other. Introgressed forms (a–r) are more loosely grouped together or near *P. subintegra* or *P. stansburiana*.

Discriminant Function Analysis

Univariate and multivariate F-tests conducted as part of DFA indicated that 14 of 15 characters used were significant at or below the .001 level of significance. Sepal length/width ratio was the only character that did not produce a high F-number. This was true of all character combinations and a priori grouping assumptions.

Two-dimensional graphical illustrations of canonical factor scores often used to show groupings derived from DFA are partially dependent on initial group assignments. For this reason, DFAs were first run on data matrices in which groups were assigned according to the 27 collection sites for each plant, rather than a preconceived notion of the classification of each plant. A series of 27-group analyses were run (Figs. 6A, 6D, 6G) using the 15-, 7-, and 4-character sets. This clearly showed that the data naturally fall into at least three or four groups, depending on how many characters are used.

Results of the 27-group DFAs were used to reclassify each plant into one of three or four groups. Bylas, Burro Creek, Horseshoe Lake, and Verde Valley (sites **D**, **E**, **F**) plants were classified as *P. subintegra*. Plants collected from Jerome, Skull Valley, and Sonoita were placed in *P. stansburiana*. All other plants were placed in "Verde" or "Tonto" introgressed forms, or were combined together in a single group of introgressed forms. Figure 6 illustrates results of nine DFA analyses with three character suites, each analyzed on two additional a priori grouping assumptions.

Character suites containing as few as two characters (e.g., hypanthium-pedicel length

TABLE 3. Characteristics of 27 groups of sampled *Purshia* spp. Mean values and standard errors (in parentheses) are listed for 15 measured characters of 27 sample sites and 216 specimens.

Character	*Purshia subintegra*	"Verde"	"Tonto"	*Purshia stansburiana*
Leaf pubescence	2.075	1.538	1.330	1.393
(scale 1–5)	(0.052)	(0.055)	(0.085)	(0.091)
Leaf lobes	0.721	3.696	3.988	3.734
(count)	(0.074)	(0.135)	(0.109)	(0.083)
Leaf glands	0.020	0.863	0.200	1.000
(presence-absence)	(0.012)	(0.042)	(0.083)	(0.000)
Hypanthium-pedicel glands	0.107	0.891	0.400	1.000
(presence-absence)	(0.028)	(0.046)	(0.112)	(0.000)
Hypanthium-pedicel length	5.098	9.170	10.113	6.620
(mm)	(0.073)	(0.266)	(0.674)	(0.151)
Hypanthium width	2.447	2.154	3.258	2.945
(mm)	(0.033)	(0.039)	(0.115)	(0.071)
Hypanthium-pedicel length/width	2.132	3.591	3.147	2.275
	(0.031)	(0.086)	(0.213)	(0.043)
Sepal length	3.565	4.050	3.961	4.886
(mm)	(0.042)	(0.069)	(0.150)	(0.115)
Sepal width	2.818	3.283	3.498	4.295
(mm)	(0.031)	(0.056)	(0.102)	(0.089)
Sepal length/width	1.282	1.248	1.390	1.151
	(0.014)	(0.018)	(0.126)	(0.022)
Petal length	8.494	9.880	10.678	11.246
(mm)	(0.109)	(0.164)	(0.342)	(0.215)
Petal width	5.730	8.357	8.289	10.307
(mm)	(0.087)	(0.219)	(0.305)	(0.288)
Petal length/width	1.536	1.226	1.311	1.147
	(0.201)	(0.027)	(0.024)	(0.022)
Stamens	48.582	67.404	66.585	88.961
(count)	(0.879)	(1.760)	(3.245)	(4.035)
Pistils	3.465	5.364	5.222	5.486
(count)	(5.364)	(0.088)	(0.204)	(0.179)

and sepal width), and essentially all other combinations of characters up to the full 15 available, consistently produced the same pattern: *P. subintegra* and *P. stansburiana* are grouped in distinct clusters, but the *P. subintegra* cluster is normally much more cohesive than the other, while both introgressed forms are usually loosely grouped in one or two clusters.

The best discrimination between groups was obtained using all 15 characters, with a 3-group assumption (Fig. 6B). There is virtually no overlap between groups, except in the case of collection site a. Table 5 lists canonical loadings for each character on each discriminant function (DF) obtained from DFA. These are useful in identifying the characters most responsible for discriminating on each of the DFs. In every DFA, leaf glandularity and lobing are the highest loading characters on DF I, and frequently load highest on the second and third DFs as well. In the 15- and 7-character suite DFAs, hypanthium-pedicel length is usually the third highest loading character.

More tightly clustered DFA plots of *P. subintegra* are taken to indicate less morphological variability in these four populations relative to the other groups. Separate DFAs and PCAs run only on the *P. subintegra* plants indicate that significant variability occurs within this group, and post-hoc identification of each plant into one of the four *P. subintegra* groups is about 50–90% accurate. In contrast, DFAs using only *P. stansburiana* and introgressed forms (i.e., no *P. subintegra*) provided poor discrimination between those groups.

Each DFA produced a set of group membership probabilities for each plant. These were used to create the tables of a priori and predicted memberships shown in Table 6. These predictions were almost always highly accurate, over 95%. In the 4-character, 4-group analysis (Table 6), DFA was only about 80% accurate for the "Verde" and "Tonto" groups, but over 95% accurate for identifying *P. subintegra* and *P. stansburiana*.

"Tonto" plants have long hypanthia-pedicels (mean 10.1 mm) and eglandular leaves, while
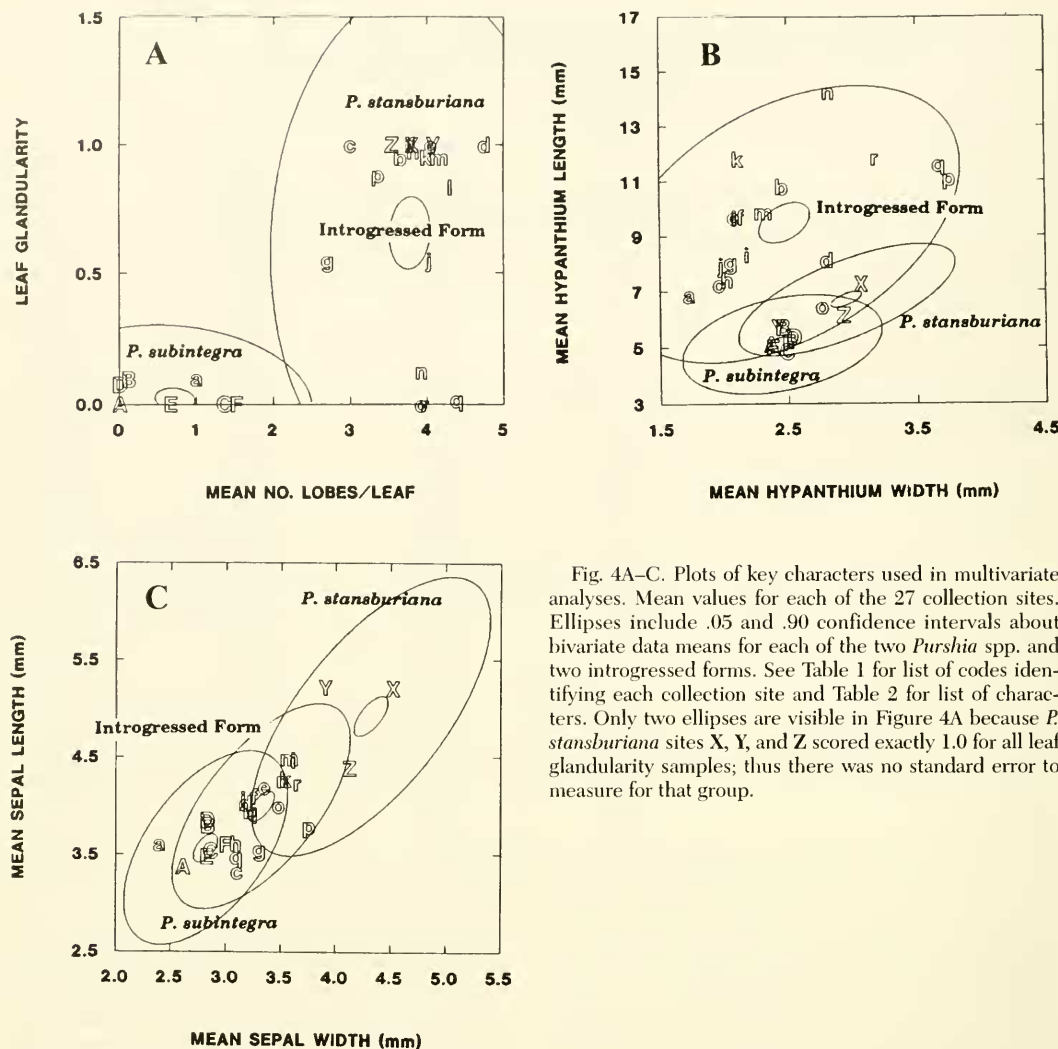
Fig. 4A–C. Plots of key characters used in multivariate analyses. Mean values for each of the 27 collection sites. Ellipses include .05 and .90 confidence intervals about bivariate data means for each of the two *Purshia* spp. and two introgressed forms. See Table 1 for list of codes identifying each collection site and Table 2 for list of characters. Only two ellipses are visible in Figure 4A because *P. stansburiana* sites **X**, **Y**, and **Z** scored exactly 1.0 for all leaf glandularity samples; thus there was no standard error to measure for that group.

"Verde" plants have slightly shorter hypanthia-pedicels (mean 9.2 mm) and glandular-punctate leaves. Generally, "Tonto" plants are found in Gila County, Arizona, on lakebed deposits around Roosevelt Lake in Tonto Creek basin. Note that Camp Verde, site **n**, is included in the "Tonto" introgressed form despite its location in Verde Valley in close proximity to the "Verde" introgressed form. This assignment resulted from inspection of previous DFAs and PCAs. Pinal Creek "Tonto" plants (site **p**) are frequently given the highest probability of belonging to the "Verde" introgressed form despite their location far away from any other "Verde" collection site (Fig. 2). Plants at these collection sites illustrate the high degree of variability in phenotypic expression of introgressed forms.

DISCUSSION

Multivariate analysis of character variation clearly indicates that the four *Purshia subintegra* populations sampled exhibit a coherent syndrome of characters. Although there is some variation between populations, the taxonomy developed by Schaack (1987b) is not supported by the analyses. Specimens claimed to be of hybrid origin by Schaack (1987a, 1987b) from among the type material collected at Burro Creek should be considered to represent *P. subintegra*. It may be speculated that leaf lobing and leaf and hypanthium-pedicel glandularity exhibited by these specimens arose from a limited exchange of genetic information with *P. stansburiana* during a period of brief proximity in the ranges of the two species.

TABLE 4. Principal components analysis of *Purshia* spp. showing factor axis loadings resulting from analysis of the full set of measured characters and two abbreviated sets. Scores from the first three factor axes are given for each character set.

15-character set	Factor axis		
	1	2	3
LOBES	0.557	0.212	0.221
STMNS	0.118	0.111	0.045
PETWDTH	0.092	0.107	0.075
PSLSFLR	0.074	0.088	0.101
SEPWDTH	0.041	0.059	0.017
PETLGTH	0.021	0.043	0.056
SEPLGTH	0.010	0.045	0.025
LEAFGLAN	0.085	0.259	0.103
HYPLGTH	0.054	0.050	0.256
HYPWDTH	0.010	−0.016	−0.007
HYPGLAN	0.076	0.304	0.090
PETRAT	−0.050	−0.040	−0.015
SEPRAT	−0.013	−0.019	0.004
LEFPUB	−0.057	−0.072	−0.063
HYPRAT	0.024	0.035	0.188
% of total variance	32.432	22.723	17.367
7-character set			
LOBES	0.569	0.252	0.185
SEPWDTH	0.044	0.067	0.013
SEPLGTH	0.015	0.055	0.015
HYPWDTH	0.006	−0.014	0.018
LEAFGLAN	0.086	0.274	0.073
HYPLGTH	0.066	0.081	0.257
HYPGLAN	0.077	0.316	0.069
% of total variance	43.075	31.713	13.894
4-character set			
LOBES	0.590	0.177	0.197
LEAFGLAN	0.101	0.166	0.084
HYPGLAN	0.091	0.302	0.074
HYPLGTH	0.075	0.057	0.263
% of total variance	50.081	20.615	16.208

Whatever gene exchange occurred must have occurred many generations ago and did not sufficiently influence the values taken by Burro Creek *Purshia* plants in respect to the 15 characteristics evaluated here to differentiate these specimens from *P. pinkavae* represented by the specimens I collected at Bylas.

Anderson (1986) reported that the Horseshoe Lake population primarily comprised hybrid and introgressed forms that were in the process of being "swamped out" by *P. stansburiana*. It is now clear that all *Purshia* plants in the area are appropriately identified as *P. subintegra* and that *P. stansburiana* is not present except perhaps at higher elevations several kilometers distant.

At Bylas, Burro Creek, and Horseshoe Lake, *P. subintegra* is unlikely to exchange genetic information with any other *Purshia* taxon. *P. subintegra* in Verde Valley is restricted to a band roughly 1 km wide and 6 km long, paralleling the Verde River east of Cottonwood, Arizona, which may extend north along a series of bluffs overlooking Verde Valley (collection site a). This isolated edaphic relict is surrounded by pockets of *Purshia* plants that appear to be intermediate in some characters between it and *P. stansburiana*, which occurs only at elevations above 1500 m. Table 7 presents a simplified chart of ecological and morphological characteristics that may be used to distinguish *P. subintegra*, introgressed forms, and *P. stansburiana*. Generally, *P. subintegra* plants have no leaf glands, 0–2 lobes per leaf, and hypanthia-pedicels about 5 mm long; *P. stansburiana* plants have abundant leaf glands, at least 3–4 lobes per leaf, and hypanthia-pedicels about 6.6 mm long; introgressed forms leaves are glandular or not, have at least 3–4 lobes per leaf and hypanthia-pedicels about 9–10 mm long. Approximately 86% of leaves of "Verde" forms are glandular, while only 20% of "Tonto" leaves are glandular.

"Verde" and "Tonto" plants are rare to uncommon throughout the Verde and Salt River basins between 600 and 1500 m elevation. In Verde Valley, "Verde" plants are found on the same Verde Formation soils as support *Purshia subintegra*. Collection site i, of "Verde" plants from Verde Valley, occurs on sandy reddish soils derived from weathered Supai Formation sandstones. Some of the "Tonto" collection sites occurred on Quaternary alluvium derived from weathered granites and schists, some occurred on limy soils derived from Tertiary lakebed deposits, and some on conglomerates composed of volcanic ashes and mudflows. Most of these sites were characterized by sparsely vegetated sterile or poor soils.

Fitts et al. (1992) attempted to perform reciprocal crossing experiments involving *P. subintegra* and *P. stansburiana* with pollen from what the investigators believed to be *P. stansburiana* in a dry wash only a few score meters from their *P. subintegra* study subjects at Dead Horse Ranch State Park (about 2 km north of Cottonwood), and approximately 3 km northwest of Verde Valley *P. subintegra* sites D, E, and F (Fig. 2). Reciprocal crosses resulted in 50% seed set, compared with 80% for within-species outcrossed flowers and 20% for

A

15 CHARACTER SET

B

7 CHARACTER SET

C
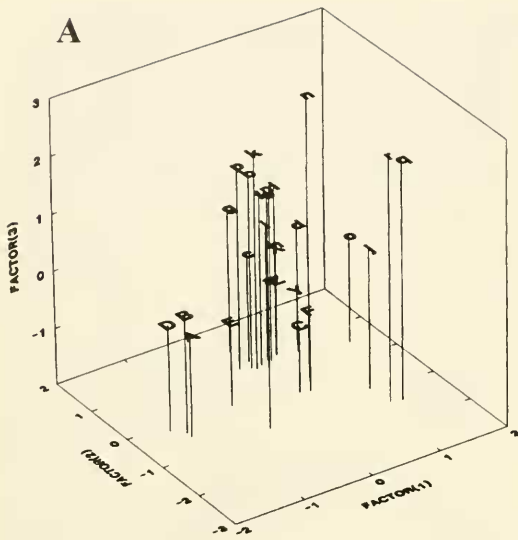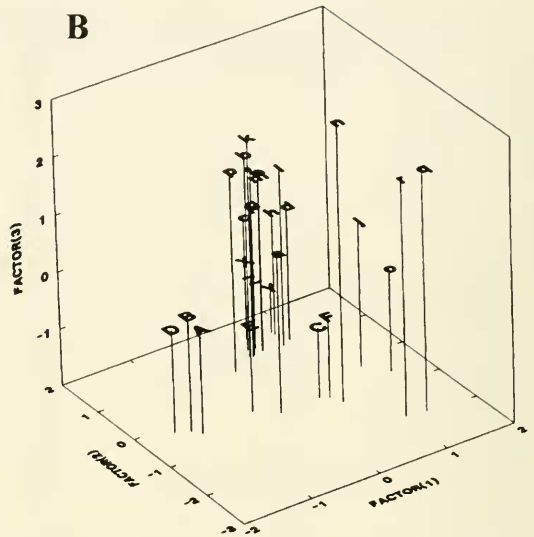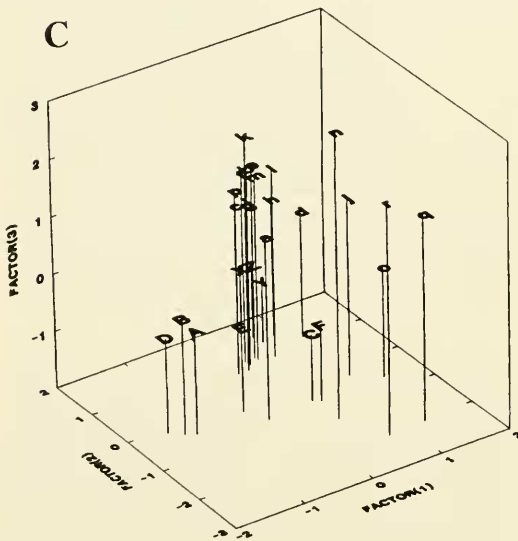
4 CHARACTER SET

Fig. 5A–C. Three-dimensional plots of mean factor scores for each of the 27 collection sites of *Purshia* spp. and introgressed forms included in the PCA on the first three factor axes. See Table 1 for locations and descriptions of sites corresponding to letter codes and Table 4 for lists of characters used in the three sets.

self-pollinated flowers. Seeds appeared normal and viable, although no attempt has been made to study viability of the seeds produced from reciprocal crosses (V. Tepedino personal communication June 1992).

Identity of the plants from which *P. subintegra* pollen was taken is clear, but the question remains whether reciprocal crossing experiments were conducted with pollen from *P. stansburiana* or "Verde" introgressed forms. U.S. Fish and Wildlife Service botanists Sue Rutman and Bruce Palmer collected four post-reproductive specimens of *Purshia* sp. in November 1992 from the same dry wash used by Fitts et al. in
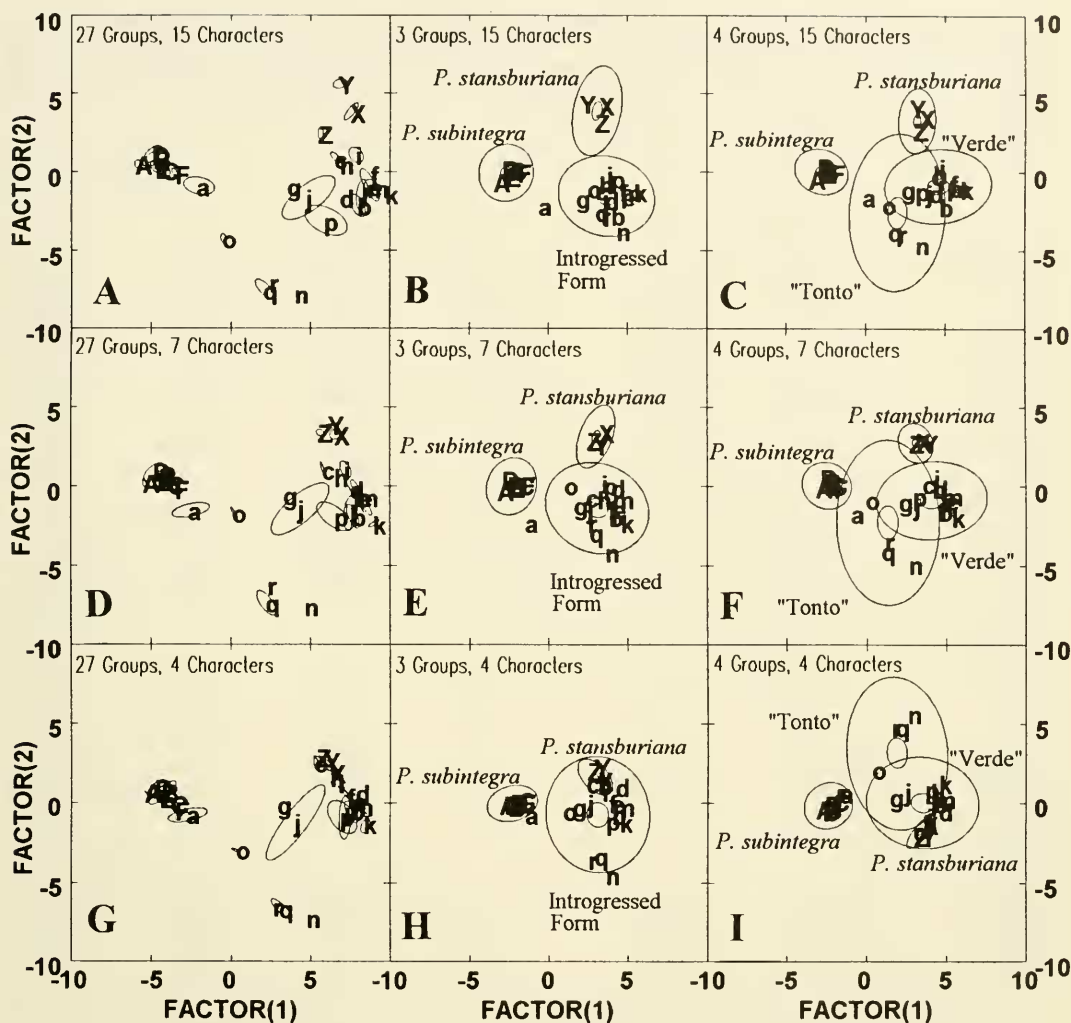
Fig. 6A–I. Plots of mean factor scores for each of the 27 collection sites of *Purshia* spp. and introgressed forms included in nine separate DFAs on the first two discriminant functions. Ellipses representing .90 confidence intervals about bivariate data means for each of the 27-group analyses (A, D, G), and .90 and .05 confidence interval ellipses for the 3- (B, E, H), and 4- (C–I) groups of *Purshia* spp. and introgressed forms.

their pollination studies. Like Fitts et al., Rutman and Palmer identified these specimens as *P. stansburiana*, based primarily on glandularity and leaf lobing. As already stated, I believe there is no *P. stansburiana* in Verde Valley; the species is restricted to elevations over 1500 m. The four pressed specimens were rehydrated and meaningful data were obtained from hypanthia-pedicels that were dried but persisted in place. Two of the specimens had one or two fresh flowers in anthesis. Data collected from these specimens—including leaf glandularity, leaf lobing, hypanthium glandularity, hypanthium length, hypanthium width, sepal length, and sepal width—were

added to the data set used for previous analyses. The four new specimens were classified through DFA as *P. stansburiana* or the "Verde" introgressed form, but not as *P. subintegra* or the "Tonto" introgressed form, depending on which a priori grouping assumptions were used. When the four new specimens were placed in their own group and added to the 27-group analysis discussed above, they were easily distinguished from *P. stansburiana* and placed in the "Tonto" introgressed form group, primarily based on hypanthium dimensions.

Whether Fitts et al. (1992) used *P. stansburiana* or plants more representative of what should be called an 'introgressed form', their

TABLE 5. Canonical within-groups structures obtained by discriminant function analysis of *Purshia* spp. Canonical loadings resulting from analysis of the full set of measured characters and two abbreviated sets. Each character set is subjected to analysis under three a priori grouping assumptions: 27 groups (one for each specimen collection site), 3 groups (*Purshia subintegra*, introgressed forms, *P. stansburiana*), 4 groups (*P. subintegra*, introgressed form "Verde," introgressed form "Tonto," *P. stansburiana*).

15-character set						
	27-group analysis		3-group analysis		4-group analysis	
DF	1	2	1	2	1	2
LEAFGLAN	0.594	0.444	0.457	0.294	0.609	0.494
HYPGLAN	0.256	0.145	0.338	0.180	0.360	0.233
LEFPUB	−0.101	0.078	−0.196	−0.040	−0.175	−0.008
LOBES	0.500	−0.300	0.632	0.061	0.579	−0.043
HYPLGTH	0.309	−0.552	0.411	−0.314	0.374	−0.439
HYPWDTH	0.030	−0.090	0.057	0.199	0.019	0.094
HYPRAT	0.234	−0.400	0.336	−0.406	0.330	−0.444
SEPLGTH	0.154	0.202	0.225	0.373	0.207	0.341
SEPWDTH	0.224	0.198	0.340	0.532	0.299	0.455
SEPRAT	−0.045	−0.056	−0.037	−0.117	−0.040	−0.131
PETLGTH	0.159	0.021	0.255	0.210	0.228	0.145
PETWDTH	0.281	0.107	0.428	0.375	0.388	0.315
PETRAT	−0.158	0.001	−0.251	−0.122	−0.240	−0.119
PSLSFLR	0.272	−0.059	0.439	0.106	0.408	0.048
STMNS	0.264	0.176	0.318	0.385	0.288	0.335
7-character set						
LEAFGLAN	0.639	0.531	0.533	0.304	0.690	0.498
HYPGLAN	0.276	0.201	0.392	0.180	0.406	0.226
LOBES	0.545	−0.249	0.726	0.003	0.637	−0.118
HYPLGTH	0.341	−0.633	0.461	−0.425	0.403	−0.551
HYPWDTH	0.036	−0.068	0.071	0.234	0.015	0.107
SEPLGTH	0.164	0.229	0.269	0.425	0.235	0.369
SEPWDTH	0.241	0.267	0.406	0.604	0.337	0.490
4-character set						
LEAFGLAN	0.651	0.720	0.534	0.602	0.719	−0.612
HYPGLAN	0.281	0.255	0.394	0.358	0.426	−0.260
LOBES	0.565	−0.362	0.730	0.032	0.685	0.289
HYPLGTH	0.357	−0.641	0.466	−0.796	0.425	0.621

experiment indicated a significant potential for gene exchange outside of *P. subintegra*.

The introgressed forms, "Verde" and "Tonto," are nearly identical to *P. stansburiana* in leaf lobing, leaf vestiture, stature, and number of pistils per flower. They are only intermediate in leaf and hypanthium-pedicel glandularity, sepal and petal dimensions, and number of stamens per flower. Length and width of the hypanthium-pedicel in the introgressed forms are not intermediate between *P. subintegra* and *P. stansburiana*; hypanthia are consistently longer and, for most populations, narrower. Introgressed forms do not appear to be closer to *P. subintegra* in any of the scored or measured characters. Cooperrider (1957) and Anderson and Harrison (1979) studied a similar situation in *Quercus marilandica*, *Q.*

velutina, and a putative hybrid. Anderson and Harrison (1979) used morphological data and PCA to test Cooperrider's (1957) use of Anderson's (1949) hybrid index to determine the degree of introgression between putative hybrid and putative parent species in Iowa. Data collected by Anderson and Harrison in Oklahoma showed that, in some characters, the hybrid was definitely intermediate, while in other characters the hybrid was more similar to *Q. velutina* than *Q. marilandica*. Ordinations of data in PCA showed putative hybrids were clearly more similar to *Q. velutina*. On the surface one would expect that putative hybrids are backcrossing with *Q. velutina*, but not with *Q. marilandica*. Anderson and Harrison, pointing out that they can find no ecological reason why backcrosses with *Q. marilandica* should

TABLE 6. Post-hoc classification of cases in groups from discriminant function analysis. A priori classifications are on the left side, predicted group memberships on the top.

216 cases, 15 characters, 3 groups

Actual group	P. stansburiana	Introgressed form	P. subintegra	Total
P. stansburiana	29	0	0	29
Introgressed form	1	62	2	65
P. subintegra	0	0	122	122
Total	30	62	124	216

216 cases, 15 characters, 4 groups

Actual group	P. stansburiana	"Verde"	"Tonto"	P. subintegra	Total
P. stansburiana	28	0	0	0	28
"Verde"	0	44	0	2	46
"Tonto"	1	0	19	0	20
P. subintegra	0	0	0	122	122
Total	29	43	19	124	216

216 cases, 4 characters, 3 groups

Actual group	P. stansburiana	Introgressed form	P. subintegra	Total
P. stansburiana	29	0	0	29
Introgressed form	13	49	3	65
P. subintegra	0	0	122	122
Total	42	49	125	216

216 cases, 4 characters, 4 groups

Actual group	P. stansburiana	"Verde"	"Tonto"	P. subintegra	Total
P. stansburiana	28	0	0	0	28
"Verde"	9	32	2	3	46
"Tonto"	0	4	16	0	20
P. subintegra	2	0	0	120	122
Total	39	36	18	123	216

not be just as prevalent as those with *Q. velutina*, argue instead that the problem lies in not properly delineating the range of variation in putative parents, putative hybrids, and introgressed forms. They found characters with non-intermediate dimensions, but in every case these were closer to one putative parent than the other and not, as described here for hypanthium-pedicel dimensions, quite different from both putative parents. This could be accounted for by several factors including natural variation, heterosis, and linked gene controls of simple characters. No breeding experiments involving *P. subintegra* and *P. stansburiana* have yet been carried out so that we may describe the quantitative characteristics of an actual hybrid. It has only been assumed so far that a hybrid should possess a morphology roughly intermediate between the parents. The close proximity of some "Verde" plants to *P. subintegra* suggests the opportunity for hybridization exists now, although data pre-

sented here do not indicate which of the sampled plants, if any, represent F_1 hybrids.

Results obtained in this study of *Purshia* indicate that while it is reasonably simple to determine what is *P. subintegra*, it is not always possible to distinguish what have been referred to as 'introgressed forms' from *P. stansburiana*. Results of Anderson and Harrison (1979), in a situation similar to that described here, might suggest that we consider introgressed forms a part of the natural variation inherent in locally adapted *P. stansburiana* genomes, and not, as has been assumed by many, a result from a predominance of backcrosses with *P. stansburiana*. Why then are forms as similar to *P. stansburiana*, as described above, found in such proximity to *P. subintegra* at Dead Horse Ranch, and how is it that *P. subintegra* in Verde Valley has remained morphologically distinct despite what appears to be ample opportunity for extensive hybridization?

TABLE 7. Reliable characters useful in discriminating between *P. subintegra*, *P. stansburiana*, and introgressed forms. Quantities in parentheses are mean values taken from Table 3. Other data are based on author's observations and Anderson (1986).

Character	Purshia subintegra	"Verde"	"Tonto"	Purshia stansburiana
Distribution	640–1065 m elevation, northwest of Bylas, Graham Co.; north of Burro Cr., Mohave Co.; Horseshoe L., Maricopa and Yavapai cos.; east of Cottonwood, Yavapai Co.	1020–1385 m elevation, Verde Valley, Yavapai Co.	725–1015 m elevation, near Camp Verde, Yavapai Co.; Tonto Basin and south of Globe, Gila Co.	Statewide (except southwestern quarter), generally above 1500 m elevation
Ecology	Restricted to limey soils derived from weathered Tertiary lakebed limestones	Mostly restricted to limey soils derived from weathered Tertiary lakebed limestones, occasionally on Supai Formation sandstones	Limey soils of weathered lakebed limestones; other limestone formations, soils derived from volcanics and alluvial materials	Various
Growth form	Shrub, up to 1 m tall, stems widely and sparingly branching from the base	Shrub, 1–2 m tall when mature, widely and sparingly branched from the base	Shrub, 1–2, or sometimes 3 m tall when mature, widely and sparingly branched from the base	Shrub, 3–5 m tall when mature, stems erect, branching from the base
Leaf shape	Entire or 1–2 lobes (0.7 lobes per leaf)	3–5 lobes (3.7 lobes per leaf	3–5 lobes (4.0 lobes per leaf)	3–5 lobes (3.7 lobes per leaf)
Leaf vestiture	Very densely pubescent on lower surface, less pubescent on upper surface	Very densely pubescent on lower surface, less pubescent to bare on upper surface	Very densely pubescent on lower surface, less pubescent to bare on upper surface	Very densely pubescent on lower surface, less pubescent to bare on upper surface
Leaf glandularity	Usually none, rarely with impressed punctate glands (2% glandular)	Usually glandular (86% glandular)	Usually not glandular (20% glandular)	Abundantly glandular (100% glandular)
Hypanthia-pedicels	Short, usually not glandular, rarely with stalked glands (5.1 mm long, 2.4 mm wide, 11% glandular)	Long, usually with stalked glands (9.2 mm long, 2.2 mm wide, 89% glandular)	Long, usually without stalked glands (10.1 mm long, 3.2 mm wide, 40% glandular)	Short, with abundant stalked glands (6.6 mm long, 2.9 mm wide, 100% glandular)
Sepals	Short and narrow (3.6 mm long, 2.8 mm wide)	Long and narrow (4.1 mm long, 3.3 mm wide)	Short and wide (4.0 mm long, 3.5 mm wide)	Long and wide (4.9 mm long, 4.3 mm wide)
Petals	Short and very narrow (8.5 mm long, 5.7 mm wide)	Long and wide (9.9 mm long, 8.4 mm wide)	Long and wide (10.7 mm long, 8.2 mm wide)	Very long and very wide (11.3 mm long, 10.3 mm wide)
Pistils	3–4 (3.5 per flower)	4–6 (5.4 per flower)	4–6 (5.2 per flower)	4–6 (5.5 per flower)
Stamens	(48.6 per flower)	(67.4 per flower)	(66.6 per flower)	(89.0 per flower)

Deciding whether the introgressed forms, "Verde" and "Tonto," should be considered as such, or, alternatively as manifestations of a broader concept of *P. stansburiana*, is not vital to the need that prompted this study: namely, a means of accurately identifying *P. subintegra*

for the purpose of determining what is and is not to be considered endangered under federal law.

No nomenclatural revisions or additions to the classification of *Purshia* are proposed; plants reported here as introgressed forms

should be regarded as such unless carefully controlled crossing and backcrossing experiments are conducted that clearly show resulting progeny are essentially identical to "Verde" and "Tonto" plants in the field. I recommended in 1986 that most fruitful results for the interpretation of morphological variation in *P. subintegra* would be obtained from a 'common garden' experiment. Under more carefully controlled conditions than may be found in the field, it should be possible to trace genetic bases for morphological characters relied on so heavily in this paper. Had such a study been initiated at that time, we may very well be enjoying the lucidity provided by early results.

Hybrid formulae for nothotaxa have not yet been validly published for the introgressed forms and should not be until their origins are firmly established. Protective measures of the Endangered Species Act should be applied to those forms that conform to the *P. subintegra* character list in Table 7, but not to plants conforming to the characteristics listed for the introgressed forms or to *P. stansburiana*.

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